

HOST USE BY SYMPATRIC COWBIRDS IN SOUTHEASTERN ARIZONA

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ABSTRACT.—Sympatric avian brood parasites may compete for the same nests to parasitize. Host-resource partitioning, or “alloxenia,” is exhibited by several Old World cuckoos where they are sympatric in Africa, Japan, and Australia. I examined host use by sympatric Brown-headed Cowbirds (*Molothrus ater*) and Bronzed Cowbirds (*M. aeneus*) from 1997 to 1999 in pine-oak and montane riparian forests in southeastern Arizona. Bronzed and Brown-headed cowbirds partitioned hosts by host body size. Brown-headed Cowbirds did not parasitize larger hosts (i.e., Western Tanager, *Piranga ludoviciana*; and Hepatic Tanager, *P. flava*), while Bronzed Cowbirds did not parasitize smaller hosts (i.e., Painted Redstarts, *Myioborus pictus*; and Bell’s Vireos, *Vireo bellii*). Although there was some host overlap (only 2/7 parasitized host species were parasitized by both cowbird species), only 3/48 nests (all Plumbeous Vireo, *V. plumbeus*) contained eggs of both parasite species. Parasitism by sympatric cowbirds in southeastern Arizona appears to fit the pattern of alloxenia. Received 16 October 2003, accepted 13 June 2005.

Avian obligate brood parasites do not build nests, but lay their eggs in the nests of other species, the “hosts,” which raise young parasites (Friedmann 1929, Davies 2000). Fitness of obligate brood parasites is directly related to choosing suitable hosts. Such hosts lack effective anti-parasite behaviors (e.g., egg rejection; Rothstein 1990), effectively incubate the parasite’s eggs, and feed the parasite’s young an appropriate diet (Middleton 1991). Interference by other brood parasites at an already parasitized host nest—in the form of egg puncturing, egg removal, or multiple parasitisms—can reduce parasite fitness (Peer and Sealy 1999, Nakamura and Cruz 2000, Trine 2000).

Partitioning of hosts may reduce the potential costs of interference competition between sympatric brood parasites. Sympatric brood parasitic cuckoos (*Cuculus*, *Chrysococcyx*, *Clamator*, *Eudynamys*, *Oxylophus*, *Scythrops*) in Africa, Australia, and Japan partition their primary hosts, possibly reducing competition for nests (Friedmann 1967, Payne and Payne 1967, Brooker and Brooker 1989, 1992; Higuchi 1998). Friedmann (1967) coined the terms “alloxenia” to describe host partitioning by obligate brood parasites in sympatry and “homoxenia” to describe overlap in host

use. In contrast to studies of Old World cuckoos, there is little information on host use by sympatric New World brood parasites (but see Carter 1986, Peer and Sealy 1999, Mermoz and Fernández 2003).

The brood-parasitic Brown-headed (*Molothrus ater*) and Bronzed (*M. aeneus*) cowbirds are sympatric in the southern United States and northern Mexico (Lowther 1993, 1995). Bronzed and Brown-headed cowbirds are considered host generalists that have been recorded parasitizing 94 and 230 different host species, respectively; they overlap in the parasitism of 37 species (Sealy et al. 1997, Ortega 1998; P. E. Lowther pers. comm.). The reproductive success of female cowbirds is directly related to the number of eggs laid in appropriate host nests during the host’s laying period (Ortega 1998). Body size of the host also may affect the reproductive success of parasites: relatively small hosts may not be able to effectively incubate the larger eggs of parasites (Davies and Brooke 1988, McMaster and Sealy 1997, Peer and Bollinger 1997), whereas large hosts may be able to grasp and eject cowbird eggs (Rothstein 1975, Rohwer and Spaw 1988). Host selection may differ between the two cowbird species because Bronzed Cowbirds are larger (female mass = 56.9 g) than Brown-headed Cowbirds (female mass = 32.0 g; Johnsgard 1997).

Similar to sympatric species of brood parasites elsewhere (e.g., Brooker and Brooker 1992), coexisting cowbirds may reduce potential interspecific competition for nests through

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differential host use (i.e., allolexenia). I tested the hypothesis that sympatric Bronzed and Brown-headed cowbirds exhibit host-size allolexenia in southeastern Arizona.

METHODS

Study sites.—My study was conducted in the Huachuca Mountains (elevation 1,500–2,450 m, 31° 26' N, 110° 20' W) of southeastern Arizona near Sierra Vista. During the breeding seasons (May–July) of 1997–1999, I examined host use by Bronzed and Brown-headed cowbirds at four discrete study sites (~20 ha each) in two distinct habitat types: Reef Townsite and Sawmill Canyon in pine-oak woodlands, and Garden Canyon and Huachuca Canyon in montane riparian forests. The two montane riparian forest sites were 7 km apart, and the pine-oak woodland sites were 9 km apart. Of the four sites, Garden Canyon and Sawmill Canyon were closest to one another (1.5 km apart).

The overstory in the pine-oak woodland sites was dominated by ponderosa (*Pinus ponderosa*), southwestern white (*P. strobiformis*), Apache (*P. latifolia*), and Chihuahuan (*P. chihuahuana*) pines. Dominant shrubs of the understory included silverleaf (*Quercus hypoleucoides*) and netleaf (*Q. reticulata*) oaks, and, especially at Reef Townsite, manzanita (*Arctostaphylos pungens*).

Montane riparian habitat is narrow, linear (<200 m wide), and extends along an elevational gradient (1,500–1,800 m) surrounded by a matrix of xeric habitats: pinyon-juniper, desert scrub, montane chaparral, desert grassland, and Madrean oak woodlands. Primary canopy species included Fremont cottonwood (*Populus fremontii*), velvet ash (*Fraxinus velutina*), Arizona sycamore (*Platanus wrightii*), bigtooth maple (*Acer grandidentatum*), and Arizona walnut (*Juglans major*). Common in the understory were Arizona white (*Q. arizonica*) and netleaf oaks, Arizona madrone (*Arbutus arizonica*), silk-tassel (*Garrya wrightii*), poison ivy (*Rhus radicans*), and canyon grape (*Vitis arizonica*).

Frequency of host parasitism, impact, and cowbird reproductive success.—Searches for potential host nests were conducted daily from 20 May to 15 July at Reef Townsite and Sawmill Canyon during 1997–1999, and in Huachuca Canyon and Garden Canyon during

1998–1999. Potential nests included those of all known host species (Ortega 1998) and congeners of known hosts. Nests were monitored at least once every 3 days, either directly or with a 6-m telescoping mirror-pole. I defined the frequency of parasitism as the proportion of parasitized nests. Clutch initiation was determined by backdating from the hatching date, using published incubation information (Ehrlich et al. 1988). The frequency of cowbird and host egg laying was standardized into 10-day periods across the total pool of nests. Cowbird egg-laying patterns then were compared with host clutch initiation by size classes of hosts (small: <10 g; medium: 10.0–29.9 g; large: >30 g).

Statistical analysis.—To determine whether Bronzed and Brown-headed cowbirds laid their eggs randomly (i.e., the “shotgun” approach; Kattan 1997) among host nests, I compared cowbird laying patterns to both a typical Poisson distribution (Preston 1948, Mayfield 1965, Elliott 1977, Kattan 1997, Trine 2000) and an adjusted Poisson distribution (Lowther 1984, Lea and Kattan 1998). Unparasitized nests are a special case because some of them may be found by cowbirds and not selected, or found too late in the egg-laying cycle to parasitize (Lowther 1984, Lea and Kattan 1998). Following Lea and Kattan (1998), I calculated the proportion of nests without cowbird eggs based on the distribution of nests with cowbird eggs. A Poisson distribution adjusted for zero-class parasitism can serve as a more conservative measure of cowbird egg-laying patterns, where a significant departure of the observed distribution from the Poisson suggests that cowbirds target nests. I used the Kolmogorov-Smirnov test (Zar 1984) to compare the distribution of Bronzed and Brown-headed cowbird egg laying, nonparametric rank sum tests to compare central tendencies when data were not normally distributed, and likelihood tests (*G*-tests) adjusted with William’s correction (Sokal and Rohlf 1981). Unless otherwise stated, all values are reported as mean ± SD; statistical significance was set at $P = 0.05$. For statistical analysis, I used the software package JMP (SAS Institute, Inc. 1995).

RESULTS

Parasitism frequency.—I monitored 220 nests of 15 species (Table 1); 8 species were

TABLE 1. Frequency of Bronzed and Brown-headed cowbird parasitism, Huachuca Mountains, Arizona, 1997–1999.

Host species	Mass (g) ^a	Total nests <i>n</i> (%)	Nests parasitized	
			Bronzed Cowbird <i>n</i> (%)	Brown-headed Cowbird <i>n</i> (%)
Hosts parasitized by both cowbird species				
Hutton's Vireo	11.6	6 (2.7)	3 (50.0)	2 (33.3)
Plumbeous Vireo	16.6	68 (30.9)	7 (10.3)	22 (32.3)
Subtotal		74 (33.6)	10 (13.5)	24 (32.4)
Hosts parasitized by Bronzed Cowbirds only				
Warbling Vireo	14.8	1 (0.4)	1 (100)	
Western Tanager	28.1	5 (2.3)	1 (20.0)	
Hepatic Tanager	38.0	8 (3.6)	6 (75.0)	
Subtotal		14 (6.4)	8 (57.1)	
Hosts parasitized by Brown-headed Cowbirds only				
Painted Redstart	7.9	7 (3.2)		1 (14.3)
Bell's Vireo	8.5	12 (5.4)		8 (75.0)
Subtotal		19 (8.6)		9 (47.4)
Species not parasitized				
Buff-breasted Flycatcher	7.9	16 (7.3)		
Western Wood-Pewee	12.8	37 (16.8)		
Yellow-eyed Junco	20.4	8 (3.6)		
Greater Pewee	27.2	28 (12.7)		
Black-headed Grosbeak	42.2	18 (8.2)		
Cassin's Kingbird	45.6	3 (1.4)		
Mexican Jay	124.0	1 (0.4)		
Steller's Jay	128.0	2 (0.9)		
Subtotal		113 (51.4)		
Total ^b		220 (100)	18 (8.2)	33 (15.0)

^a Bird mass data from Dunning (1993).

^b Although cowbirds parasitized 48 nests, the overlapping parasitism at three Plumbeous Vireo nests raises the total to 51 instances of nest parasitism among the 48 nests.

not parasitized ($n = 113$ nests) and 7 species were parasitized ($n = 107$ nests of host species; $n = 45$ at Reef Townsite, 21 at Sawmill Canyon, 22 at Huachuca Canyon, and 19 at Garden Canyon). Forty-five percent (48/107) of all host nests were parasitized; two host species were parasitized by both cowbird species (Hutton's Vireo, *Vireo huttoni*; and Plumbeous Vireo, *Vireo plumbeus*), and three nests (all Plumbeous Vireo) contained at least one egg of both cowbird species (Table 1). For hosts parasitized by both species, Bronzed Cowbird parasitism (13.5%, 10/74) was less than half that of Brown-headed Cowbirds (32.4%, 24/74; Table 1). Only Bronzed Cowbirds parasitized Hepatic Tanager (*Piranga flava*; large host) and Western Tanager (*P. ludoviciana*; high end of medium-size class), and only Brown-headed Cowbirds parasitized

Painted Redstart (*Myioborus pictus*) and Bell's Vireo (*Vireo bellii*; Table 1). Two of the medium-sized hosts (Hutton's Vireo, *Vireo huttoni*, and Plumbeous Vireo) were parasitized by both cowbird species, and the Warbling Vireo (*Vireo gilvus*) was parasitized only by the Bronzed Cowbird (Table 1).

Potential host nests monitored, but not parasitized, included those of Buff-breasted Flycatcher (*Empidonax flavifrons*), Western Wood-Pewee (*Contopus sordidulus*), Greater Pewee (*C. pertinax*), Cassin's Kingbird (*Tyrannus vociferans*), Mexican Jay (*Aphelocoma ultramarina*), Steller's Jay (*Cyanocitta stelleri*), Yellow-eyed Junco (*Junco phaeonotus*), and Black-headed Grosbeak (*Pheucticus melanocephalus*; Table 1). Other known cowbird hosts (Ortega 1998) commonly observed on at least two of the study sites, but for which

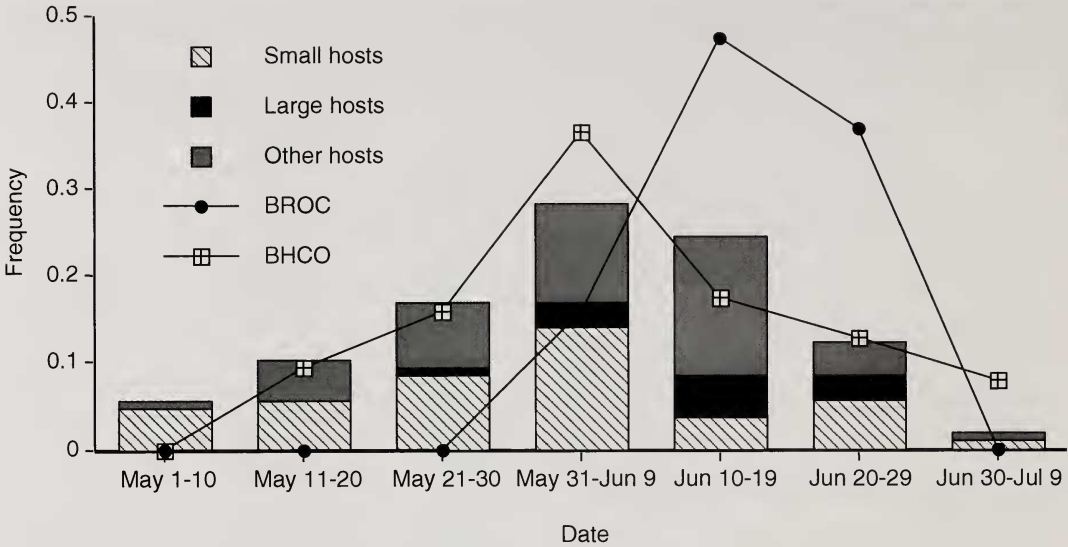


FIG. 1. Host clutch initiation (bars) and cowbird egg laying (lines) in southeastern Arizona, 1997–1999. Brown-headed Cowbirds (BHCO; 41 eggs, 29 nests) laid eggs earlier than Bronzed Cowbirds (BROCO; 21 eggs, 16 nests) ($d_{\max_{6,62}} = 29.14$; $P < 0.001$), coinciding with peak laying of small hosts (<10 g, Bell's Vireo and Painted Redstart). Bronzed Cowbirds laid later than Brown-headed Cowbirds, coinciding with peak laying of larger (38 g, Hepatic Tanager; 28 g, Western Tanager) hosts.

no nests were found, included Virginia's (*Ver-virivora virginiae*), Lucy's (*V. luciae*), Yellow-rumped (*Dendroica coronata*), Black-throated Gray (*D. nigrescens*), and Grace's (*D. graciae*) warblers; Spotted (*Pipilo maculatus*) and Canyon (*P. fuscus*) towhees; Blue Grosbeak (*Passerina caerulea*); Bullock's Oriole (*Icterus bullockii*); House Finch (*Carpodacus mexicanus*); and Lesser Goldfinch (*Carduelis psaltria*).

Parasitism by habitat.—Parasitism was significantly higher in the montane riparian forest (57%, 23/41 nests) than pine forest sites (33%, 22/66 nests; $G_{\text{adj}} = 8.26$, $df = 1$, $P = 0.004$). Parasitism frequency within replicate habitats did not differ significantly (pine-oak: $G_{\text{adj}} = 1.66$, $df = 1$, $P = 0.20$; riparian: $G_{\text{adj}} = 1.71$, $df = 1$, $P = 0.19$). In the montane riparian forest sites, Brown-headed Cowbirds parasitized 41% (17/41) of the parasitized nests, whereas Bronzed Cowbirds parasitized 24% (9/41). In the pine-oak forests, Brown-headed Cowbirds parasitized 25% (16/66) and Bronzed Cowbirds parasitized 14% (9/66) of the host nests (NB: three nests in pine-oak forest were parasitized by both species). Bronzed Cowbird parasitism was similar between the two habitat types ($G_{\text{adj}} = 0.12$, $df = 1$, $P =$

0.73), whereas Brown-headed Cowbird parasitism was higher in the riparian forests ($G_{\text{adj}} = 8.00$, $df = 1$, $P = 0.005$).

Host-size preference.—Bronzed Cowbirds parasitized larger hosts than Brown-headed Cowbirds, but both parasitized Hutton's and Plumbeous vireos. Despite this overlap, interspecific parasitism of the same nest was rare, but frequency (0.044) of double parasitism on Plumbeous Vireo nests ($n = 68$) was not different from expected (P [Bronzed] \times P [Brown-headed] = P [Bronzed + Brown-headed] = P [7/68] P [22/68] = 0.033; $\chi^2 = 0.25$, $P = 0.62$). Three Plumbeous Vireo nests were parasitized by both parasites. Two of those nests had two Bronzed Cowbird eggs and one Brown-headed Cowbird egg, whereas the third had one egg of each parasite.

Cowbird laying patterns.—The peak of cowbird laying was congruent with host clutch initiation, but the Bronzed Cowbird's laying peak was slightly later than that of the Brown-headed Cowbird (Kolmogorov-Smirnov $d_{\max_{6,62}} = 29.14$, $P < 0.001$; Fig. 1). The peak of Bronzed Cowbird laying corresponded with clutch initiation of large hosts (tanagers), while the peak of Brown-headed Cowbird laying corresponded with the peak of

TABLE 2. Number of cowbird eggs found in nests ($n = 107$) of known host species, Huachuca Mountains, Arizona, 1997–1999. Significant departures from the Poisson distribution (χ^2 goodness-of-fit; P^b) and adjusted Poisson (Kolmogorov-Smirnov D ; P^d) suggest nonrandom egg placement by cowbirds among available host nests.

	Number host nests				Total eggs	Mean ^a \pm SD	P^b	Mean ^c	D	P^d
	0 eggs	1 egg	2 eggs	3 eggs						
Brown-headed Cowbird	78	21	4	4	41	1.41 \pm 0.73	<0.001	0.74	7.3	<0.05
Bronzed Cowbird	91	12	3	1	21	1.31 \pm 0.60	0.025	0.57	7.4	<0.01
Both species combined	62	33	7	5	62	1.38 \pm 0.68	0.134	0.68	3.5	>0.50

^a Mean number of cowbird eggs observed per parasitized nest.

^b χ^2 goodness-of-fit test for cowbird egg dispersion versus Poisson distribution.

^c Mean number of cowbird eggs per nest, calculated across 107 nests available to cowbirds (following Lea and Kattan 1998).

^d Significance of Kolmogorov-Smirnov D for test of cowbird egg dispersion versus an adjusted, zero-egg class Poisson distribution.

small hosts (Bell's Vireo and Painted Redstart; Fig. 1).

Nonrandom egg laying.—Combined parasitism of both cowbird species was random with respect to the Poisson distribution (Table 2): available host nests were randomly parasitized by at least one of the two cowbird species. Evaluated individually, however, both Bronzed and Brown-headed cowbirds at my study sites laid their eggs nonrandomly among host nests (Table 2), as demonstrated by significant departures from the Poisson. Both the traditional approach (e.g., Elliott 1977) and Lea and Kattan's (1998) more conservative approach yielded the same result (Table 2). Most parasitized nests contained only one parasite egg (range 1–3) and there was no significant difference between the number of Brown-headed and Bronzed cowbird eggs laid per nest (Wilcoxon $z = 0.68$, $P = 0.75$).

DISCUSSION

In southeastern Arizona, Bronzed Cowbirds typically parasitized larger species than those parasitized by Brown-headed Cowbirds. Both cowbird species dispersed their eggs uniformly with respect to available host nests and generally avoided multiple parasitisms; congruence between the two statistical procedures (typical Poisson and adjusted Poisson distributions) strengthens this assertion. Only Bronzed Cowbirds parasitized tanagers (the two largest host species observed), while only Brown-headed Cowbirds parasitized the two smallest species (Bell's Vireo and Painted Redstarts). Two of three intermediate-sized hosts were parasitized by both cowbird species, but parasitism of the same nest by both cowbird species was rare. My results are con-

sistent with Friedmann's (1967) definition of alloxenia, albeit to a lesser degree than that observed among cuckoos, which, in sympatry, exhibit very low overlap in host use (Brooker and Brooker 1992, Higuchi 1998). An important caveat from my study is that many nests of potential hosts were not found; however, the majority of the nests of the six focal host species were likely found and monitored. My interpretation may have been different had I been able to monitor nests of other species, including those that nest high in the canopy.

Based on the host nests I was able to monitor, my results are not consistent with those indicating that homoxenia occurs among sympatric Bronzed and Brown-headed cowbirds in Texas (Peer and Sealy 1999). Compared with Peer and Sealy's study site in the mesquite grasslands and chaparral of the Texas coastal plains, southeastern Arizona has a greater diversity of hosts, especially smaller, insectivorous passerines. Although not designed as a community study, Peer and Sealy (1999) did not record Bronzed Cowbird parasitism on the smallest host species (Verdin, *Auriparus flaviceps*) in their study area, but they did find extensive overlap in parasitism. Both brood parasites laid eggs in the nests of small- to medium-sized host species (Painted Bunting, *Passerina ciris*; and Olive Sparrow, *Arremonops rufivirgatus*). Surprisingly, Bronzed Cowbirds did not parasitize some of the larger host species (Red-winged Blackbird, *Agelaius phoeniceus*; and Bullock's Oriole) that were parasitized by Brown-headed Cowbirds. No species were found to be parasitized only by Bronzed Cowbirds (Peer and Sealy 1999); however, sample sizes for some of these spe-

cies were very small. Different patterns of host use in southern Texas may have been observed had sample sizes for some of these species been larger (B. D. Peer pers. comm.).

Sympatric cuckoos in Asia, Australia, and Africa, as well as Bronzed and Brown-headed cowbirds reported here, overlap in the use of secondary hosts (Friedmann 1967, Payne and Payne 1967, Brooker and Brooker 1990, 1992; Higuchi 1998). Each of nine species of cuckoos (*Chrysococcyx* spp., *Clamator* spp., *Cuculus* spp.) in southern Africa primarily parasitize one or two hosts of 65 known host species, with only occasional host overlap (Payne and Payne 1967). Australian bronze-cuckoos (*Chrysococcyx* spp.; Brooker and Brooker 1992) and *Cuculus* spp. cuckoos in Japan (Higuchi 1998) are highly host specific in sympatry, but exhibit host overlap when allopatric.

Where parasites overlap in host use, subtle aspects of habitat selection may be involved in segregation (Southern 1954). Differential habitat selection by sympatric brood parasites has been observed among cuckoos (Friedmann 1967, Brooker and Brooker 1992) and cowbirds (Peer and Sealy 1999, Chace 2004). In Africa, three sympatric *Cuculus* spp. cuckoos exhibit a high degree of host specificity as well as habitat specificity (Friedmann 1967). Red-chested Cuckoos (*C. solitarius*) largely parasitize thrushes (*Cossypha* spp.), African Cuckoos (*C. gularis*) parasitize shrikes (*Corvinella* spp.) and drongos (*Dicrurus* spp.), and Black Cuckoos (*C. clamosus*) parasitize boubous (*Laniarus* spp.; Friedmann 1967). To some degree this host partitioning is due to habitat partitioning; Red-chested Cuckoos use the more wooded sites, whereas the African and, especially, Black Cuckoos use relatively open woodlands (Johnsgard 1997). While Bronzed and Brown-headed cowbirds occupied the same four riparian and pine-oak forests in this study, Brown-headed Cowbirds were found across a wider range of habitats than Bronzed Cowbirds (Chace 2004). At broader spatial scales, Bronzed and Brown-headed cowbirds may reduce or avoid competition for host nests through divergent habitat use.

Similar to sympatric cowbirds, sympatric cuckoos overlap extensively in diet, habitat requirements, and use of hosts (Payne and

Payne 1967, Brooker and Brooker 1992). Unlike host-generalist cowbirds, however, cuckoos tend to be host specialists (Davies 2000). Alloxenia is clearly a pattern that is most likely to occur among host and habitat specialists, and it is therefore rather interesting that we find this pattern among generalist cowbirds in Arizona.

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